

OPPORTUNISTIC BREEDING AFTER SUMMER RAINS BY ARIZONA TIGER SALAMANDERS

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Identifying factors influencing the number of times organisms breed during a lifetime and the seasonal timing of reproductive episodes is central to understanding the evolution of life history traits (Stearns 1992). In this regard, amphibian reproductive cycles are often considered adaptations to the seasonality of oviposition opportunities (Joly 1971, Lofts 1974, Salthe and Mecham 1974). This is seen in most north temperate zone amphibians that breed in temporary aquatic habitats and have annual reproductive cycles (Bishop 1947, Wright and Wright 1949). These frogs and salamanders typically come into reproductive condition once a year at the same time of year, often in spring as ephemeral habitats predictably fill from snowmelt or winter rains. Where aquatic habitats fill unpredictably or irregularly, such as in dry temperate or tropical regions, amphibians may have acyclical reproductive periods allowing them to breed opportunistically (Salthe and Mecham 1974, van Beurden 1979). Opportunistic breeding in ephemeral habitats is commonly understood as an adaptation for avoiding predaceous fish (e.g., Webb 1969, Heyer et al. 1975, Wilbur 1977, Collins and Wilbur 1979).

Tiger salamanders (*Ambystoma tigrinum* Green) range across North America and have an obligatory aquatic larval stage (Stebbins 1985). Like most ambystomatids (Bishop 1947), the six subspecies of tiger salamanders in western USA (*californiense*, *mavortium*, *nebulosum*, *diaboli*, *melanostictum*, *stebbinsi* [Collins et al. 1980, Jones et al. 1988]) all breed in late winter, spring, or even early summer at high elevations. Differences between populations in the timing of the primary breeding period correspond to differences in availability of water in their breeding

habitats (Houghton 1976). Some *A. t. mavortium* populations breed both in spring and in summer (Webb and Roueche 1971), and Tanner et al. (1971) documented *A. t. nebulosum* breeding in spring and summer in a continuously filled lake. In this study we report that *A. t. nebulosum* populations can also breed twice per year in ponds that fill with water during the winter, dry during the late spring and early summer, and refill during summer rains.

Arizona tiger salamanders (*A. t. nebulosum*) are found commonly at high elevations in montane Colorado and Utah (Stebbins 1985) and in Arizona between 1500 and 2900 m (Collins 1981). Aquatic habitats discussed in this study are in Rocky Mountain montane conifer forest (Pase and Brown 1982).

Arizona tiger salamanders breed regularly in late winter and spring following snowmelt (Sexton and Bizer 1978, Collins and Check 1983, Holomuzki 1986, Jones and Collins 1992). During the course of other fieldwork, we realized that a second breeding pattern also occurs. Here, we present observations that led us to conclude that these tiger salamanders can breed "opportunistically," defined as any breeding outside the usual late winter and early spring breeding period.

On 30 March 1990 we noted typical spring oviposition activity when we observed thousands of *A. t. nebulosum* eggs in Horseshoe Lake (34°22'53"N, 111°14'38"W) on the Mogollon Rim in central Arizona. We visited the lake again on 6 August 1990, before summer rains began. It was completely dry at this time, and we photographed thousands of desiccated salamander larvae on the lake bed. We presumed this represented elimination of the spring 1990 cohort. We sampled this lake again

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on 23 September 1990 after it had refilled following summer rains and noted several hundred small *A. t. nebulosum* larvae. Live measurements were taken from a sample of larvae on 29 September and compared to measurements taken from projections of two close-up slides of some of the dead spring cohort. We also visited other ponds in this region that had dried and refilled to gauge the extent and success of this breeding tactic.

Larvae caught in Horseshoe Lake in September were either a second cohort that hatched after summer rains, or animals from the spring cohort that survived the lake drying, presumably by burrowing. Metamorphosed tiger salamanders burrow in soft lake mud (Webb 1969), but this has not been reported for larvae or branchiate adults.

Dead larvae photographed in August averaged 51.4 mm total length (SE = 1.20 mm, $N = 35$), and larvae collected in September averaged 35.8 mm total length (SE = 0.78 mm, $N = 96$). If animals collected in September survived drying by burrowing, they should have been at least as large as the dead animals observed in August. Animals in September were, however, significantly smaller than those photographed in August ($t = 10.53$, $P < .0001$). This is a conservative test since animals photographed in August were dried and therefore smaller than at death.

We do not consider summer breeding to be the primary breeding event for this population. Because we observed several thousand eggs in March, we conclude that there was a normal spring breeding. Typical larval densities (estimated by drop-box and seining through a measured volume of water) in this part of Arizona in June are 2–75 salamanders m^{-3} (Pfennig et al. 1991). The low density of larvae we estimated in September, 0.3 salamanders m^{-3} , supports the conclusion that there was a second reproductive episode in which a small number of animals bred opportunistically in Horseshoe Lake during 1990.

Adult salamanders breeding in Horseshoe Lake in late summer 1990 were taking advantage of a newly filled habitat. At least some larvae in this second 1990 cohort overwintered successfully (M. Loeb personal observation, 4 May 1991). In 1990, Charco Tank (34°07'50"N, 110°07'32"W) in the White Mountains dried following drought conditions that also dried Horseshoe Lake. In spring 1991 we collected

larvae several centimeters larger than recently hatched salamanders in this tank, suggesting salamanders produced a second cohort in this tank following rains in summer 1990. Cottonwood Tank (34°08'43"N, 110°09'06"W) dried in June 1992. Although we did not visit this habitat later in 1992, presence of a large larva in March 1993 (before the spring cohort hatched) suggests opportunistic breeding in summer 1992.

Late-season breeding may, however, fail. Johnnie Tank (34°10'06"N, 110°04'02"W) in the White Mountains is at the same elevation as 13 ponds in the surrounding 180 km^2 . Breeding at all other ponds in this area was completed by late March in 1992 and 1993. Johnnie Tank dried in early spring 1992 and then refilled in late May after early monsoon rains. Hatchlings produced by opportunistic breeding following this refilling were all killed when the tank dried again in late June. Because the May oviposition does not overlap the usual breeding season in this area, we consider this to be opportunistic breeding.

Other evidence suggests that summer breeding is exhibited regularly in this subspecies. Metamorphosed females with yolked follicles were recorded in Arizona by Durham (1956) on 18 July on the Kaibab Plateau and by J. Collins (unpublished observation) on 11 July 1980 in the White Mountains.

Tanner et al. (1971) reported sizes of *A. t. nebulosum* larvae in Salamander Lake, a permanent lake in Utah. While following growth of larvae throughout July and August, they recorded a small size class beginning in late July, which they interpreted as evidence of a second breeding. A pattern of spring and fall breeding in permanent ponds with unpredictability in seasonal rainfall is also reported for *Triturus alpestris apuanus* in Italy (Andreone and Dore 1992). Despite the fact that we regularly visit a few dozen continuously filled ponds in Arizona, we have never observed a second breeding in one. Our observations, consistent with the hypothesis outlined below, emphasize that the natural history we are describing for *A. t. nebulosum* in Arizona differs importantly from that reported in Utah.

Webb (1969) argued that an irregular breeding pattern is among the traits that adapt *A. t. mavortium* for life in the Chihuahuan Desert in southern New Mexico; i.e., this subspecies reproduces whenever water fills the

ephemeral ponds in which it commonly breeds. *A. t. mavortium* breeds every year in ponds that fill in winter or spring, but may also breed after summer rains. Our data suggest *A. t. nebulosum* in Arizona has evolved a similar life history tactic. In general, breeding occurs following snowmelt at high elevations, but there are some conditions under which individuals will breed opportunistically following summer rains.

An amphibian larva from a spring cohort is not guaranteed sufficient time to complete development to metamorphosis in any aquatic habitat that can dry unpredictably. This is an explanation for iteroparity in most ambystomatids using temporary or "most nearly permanent" ponds (Wilbur 1977). It might be adaptive, however, for adults to take advantage of ponds whenever they refill. In contrast, late-season breeding in permanent aquatic habitats is generally not advantageous since these habitats may harbor older larvae or fish that can prey on embryos and hatchlings (Burger 1950, Reese 1968, Webb and Roneche 1971; but see Dodson and Dodson 1971 and Collins and Holomuzki 1984). Breeding after a habitat refills would be advantageous as the drying would eliminate fish or older larvae. A second advantage of breeding opportunistically arises since metamorphosis is only possible after a minimum size is achieved (Wilbur and Collins 1973), and in temporary ponds like those we report here, this size may not be attained before the pond dries; however, larvae from summer cohorts that successfully overwinter will have a growth advantage over larvae from spring clutches.

A closer examination of the life histories of other subspecies of tiger salamanders found in the arid and semiarid western USA might reveal that regular breeding in late winter and spring, with opportunistic breeding in summer, also occurs in these subspecies.

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LITERATURE CITED

- ANDREONE, E., AND B. DORE. 1992. Adaptation of the reproductive cycle in *Triturus alpestris apuanus* to an unpredictable habitat. *Amphibia-Reptilia* 13: 251-261.
- BISHOP, S. C. 1947. Handbook of salamanders. Comstock Publishing Company, Ithaca, New York. 555 pp.
- BURGER, W. L. 1950. Novel aspects of the life histories of two ambystomas. *Journal of the Tennessee Academy of Science* 25: 252-257.
- COLLINS, J. P. 1981. Distribution, habitats, and life history variation in the tiger salamander, *Ambystoma tigrinum*, in east-central and southeast Arizona. *Copeia* 1981: 666-675.
- COLLINS, J. P., AND J. CHEEK. 1983. Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. *American Zoologist* 23: 77-84.
- COLLINS, J. P., AND J. R. HOLOMUZKI. 1984. Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*). *Canadian Journal of Zoology* 62: 168-174.
- COLLINS, J. P., AND H. M. WILBUR. 1979. Breeding habits and habitats of the amphibians of the Edwin S. George Reserve, Michigan, with notes on the local distribution of fishes. *Occasional Papers of the Museum of Zoology, University of Michigan* 686: 1-34.
- COLLINS, J. P., J. B. MITTON, AND B. A. PIERCE. 1980. *Ambystoma tigrinum*: a multi-species conglomerate? *Copeia* 1980: 938-941.
- DODSON, S. I., AND V. E. DODSON. 1971. The diet of *Ambystoma tigrinum* larvae from western Colorado. *Copeia* 1971: 614-624.
- DURHAM, F. E. 1956. Amphibians and reptiles of the North Rim, Grand Canyon, Arizona. *Herpetologica* 12: 220-224.
- HEYER, W. R., R. W. MCDIARMID, AND D. L. WEIGMANN. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica* 7(2): 100-111.
- HOLOMUZKI, J. R. 1986. Effect of microhabitat on fitness components of larval tiger salamanders. *Oecologia* 71: 142-148.
- HOUGHTON, F. E. 1976. *Climates of the States. New Mexico. Climatology of the United States*, 60-15: 677-681. Gale Research Company, Detroit, Michigan.
- JOLY, J. M. J. 1971. Les cycles sexuels de *Salamandra* (L.). 1. Cycle sexuel des males. *Annales des sciences naturelles. Zoologie et Biologie Animale* 13: 451-504.
- JONES, T. R., AND J. P. COLLINS. 1992. Analysis of a hybrid zone between subspecies of the tiger salamander (*Ambystoma tigrinum*) in central New Mexico. *Journal of Evolutionary Biology* 5: 375-402.
- JONES, T. R., J. P. COLLINS, T. D. KOCHER, AND J. B. MITTON. 1988. Systematic status and distribution of *Ambystoma tigrinum stebbinsi* Lowe. *Copeia* 1988: 621-635.
- LOFTS, B. 1974. Reproduction. Pages 107-218 in B. Loftis, ed., *Physiology of the amphibia*. Academic Press, New York.
- PASE, C. P., AND D. E. BROWN. 1982. Rocky Mountain (Petran) and Madrean montane conifer forest. *Desert Plants* 4(1-4): 43-48.

- PFENNIG, D. W., M. L. G. LOEB, AND J. P. COLLINS. 1991. Pathogens as a factor limiting the spread of cannibalism in tiger salamanders. *Oecologia* 88: 161–166.
- REESE, R. W. 1968. The taxonomy and ecology of the tiger salamander (*Ambystoma tigrinum*) of Colorado. Unpublished doctoral dissertation, University of Colorado, Boulder.
- SALTRE, S. N., AND J. S. MECIAM. 1974. Reproductive and courtship patterns. Pages 310–521 in B. Lofts, ed., *Physiology of the amphibia*. Academic Press, New York.
- SEXTON, O. J., AND J. R. BIZER. 1978. Life history patterns of *Ambystoma tigrinum* in montane Colorado. *American Midland Naturalist* 99: 101–118.
- STEARNS, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford. 249 pp.
- STEBBINS, R. C. 1985. *Western reptiles and amphibians*. Houghton Mifflin Company, Boston. 336 pp.
- TANNER, W. W., D. L. FISHER, AND T. J. WILLIS. 1971. Notes on the life history of *Ambystoma tigrinum nebulosum* Hallowell in Utah. *Great Basin Naturalist* 31: 213–222.
- VAN BEURDEN, E. K. 1979. Gamete development in relation to season, moisture, energy reserve, and size in the Australian water-holding frog, *Cyclorana platycephalus*. *Herpetologica* 35: 370–374.
- WEBB, R. G. 1969. Survival adaptations of tiger salamanders (*Ambystoma tigrinum*) in the Chihuahuan Desert. Pages 143–147 in C. C. Hoff and M. L. Riedesel, eds., *Physiological systems in semiarid environments*. University of New Mexico Press, Albuquerque.
- WEBB R. G., AND W. ROUCHE. 1971. Life history aspects of the tiger salamander (*Ambystoma tigrinum mavortium*) in the Chihuahuan Desert. *Great Basin Naturalist* 31: 193–212.
- WILBUR, H. M. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. *American Naturalist* 111: 43–68.
- WILBUR, H. M., AND J. P. COLLINS. 1973. Ecological aspects of amphibian metamorphosis. *Science* 182: 1305–1314.
- WRIGHT, A. H., AND A. A. WRIGHT. 1949. *Handbook of frogs and toads of the United States and Canada*. Cornell University Press, New York. 640 pp.

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